Chimpanzee Culture Extends Beyond Matrilineal Family Units

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The "Grooming handclasp" (GHC) is one of the most well-established cultural traditions in chimpanzees. A recent study by Wrangham et al. [1] reduced the cultural scope of GHC behavior by showing that GHC-style convergence is "explained by matrilineal relationship rather than conformity" [1]. Given that we have previously reported cultural differences in GHC-style preferences in captive chimpanzees [2], we tested Wrangham et al. [1]'s alternative view in the chimpanzee populations that our original results were based on. Using the same outcome variable as Wrangham et al. [1] – proportion high-arm grooming featuring palm-to-palm clasping (PPC) – we found that matrilineal relationships neither explained within-group homogeneity nor between-group heterogeneity, thereby corroborating our original conclusion that GHC can represent a group-level cultural tradition in chimpanzees.

Given that previous studies have shown that chimpanzees learn skills from their mothers [2-4], Wrangham et al. [1] investigated whether the most common style of GHC behavior – PPC – followed a pattern based on demographic (e.g., sex, age) and/or individual (e.g., motivation to engage in GHC) factors in the chimpanzees of the Kanyawara community of Kibale National Park, western Uganda ($n_{individuals}$=35; $n_{GHC\ bouts}$=932). Their main goal was to understand how and why individuals differed in their tendency to engage in PPC [1]. By means of a series of independent statistical tests, Wrangham et al. [1] concluded that only matrilineal relationships significantly influenced individuals' PPC tendencies. In turn, the conclusion was advanced that "chimpanzees conform in their grooming styles only to their mothers, not to the larger group" [1]. Importantly, Wrangham et al. [1] keep open the option that other mechanisms might be at play in chimpanzees' GHC behavior by referring to the fact that chimpanzees at the Chimfunshi Wildlife Orphanage Trust, Zambia, seemed to reach high frequencies of PPC in the absence of long-term matrilineal relationships [1].

The Chimfunshi chimpanzees have been reported to not only exhibit high frequencies of PPC, but, notably, their GHC-style tendencies matched within groups and differed between groups [2]. Based on this group-level variation in GHC style – which cannot be accounted for

by genetic or ecological differences across groups – van Leeuwen et al. concluded that "chimpanzees' social behavior is not only motivated by innate predispositions and individual inclinations but may also be partly cultural in nature" [2]. Moreover, in contrast to Wrangham et al. [1]'s assumption, Chimfunshi houses many family units (n=16) up to the third generation. Here, we aimed to test whether chimpanzees' GHC-style may be restricted to social learning within matrilineal relationships [1] or whether chimpanzees' social learning of GHC-style extends beyond family units by re-analyzing our original data in light of possible effects of matrilineal relationships. We chose to incorporate matrilineal relationships into our original models (instead of performing separate statistical tests [1]) in order to test multiple predictors simultaneously and control for repeated observations of individuals and dyads.

Crucially, using data from two different groups across three years, and including only those chimpanzees with known matrilines (cf. [2]), we found that matrilineal relationship did not obviously contribute to variation in PPC frequency in the Chimfunshi chimpanzees (permutations of matriline within GLMM context: $\chi^2 = 3.22$, $p = 0.44$; estimated standard deviations for random intercept and random slopes of matrilines: all < 0.5; $n_{ind} = 42$, $n_{matrilines} = 16$, $n_{bouts} = 1033$). Similar results were obtained when focusing on *within*-group tendencies, i.e., no obvious effect of matrilineal relationships on chimpanzees' tendency to engage in PPC (group 1: $\chi^2 = 5.07$, p=0.44; SDs<1; $n_{ind} = 12$, $n_{matrilines} = 4$, $n_{bouts} = 230$; group 2: $\chi^2 = 2.91$, $p = 0.43$; SDs < 0.7; $n_{ind} = 30$, $n_{matrilines} = 12$, $n_{bouts} = 803$). Importantly, our originally reported group differences in PPC [2] were confirmed while controlling for the effect of matrilineal relationships ($\chi^2 = 6.33$, df = 1, $p = 0.014$; Figure 1).

Note that we analyzed our data with a random effect structure *sensu* the most established method to date (i.e., including random slopes when variation allows, in order to prevent Type I errors) [6-8]. Nonetheless, in order to preclude potentially unwarranted dismissal of matrilineal effects on PPC grooming, and based on arguments against using a (close to) maximal random effects structure ([9] referring to [10]), we additionally fitted two

more series of models with an increasingly minimal random effects structure. The first series comprised our primary model excluding the random slope terms within matrilines (thus, for matrilines, only leaving the random *intercept*). Matrilineal relationships neither obviously affected PPC tendencies *across* groups ($\chi^2 = 2.52$, p=0.40; SDs < 0.5), nor *within* groups (group 1: $\chi^2 = 2.52$, p=0.41; SDs < 1; group 2: $\chi^2 = 2.52$, p=0.35; SDs < 0.3), hence corroborating our results. The second series comprised our fixed effects model including only the random *intercepts* of subject, dyad, matriline identity, date and bout number. Again, matrilineal relationships were neither obviously affecting PPC tendencies *across* groups ($\chi^2 = 2.86$, p=0.41; SDs < 0.5). nor *within* groups (group 1: $\chi^2 = 6.96$, p=0.43; SDs < 1; group 2: $\chi^2 = 0.94$, p=0.30; SDs < 0.3). For more details, see Supplemental Information.

Note that all these results point into the same direction: contrary to the Kanyawara chimpanzees as reported by Wrangham et al. [1], the tendency to engage in PPC grooming cannot be sufficiently explained by matrilineal relationships in the Chimfunshi chimpanzees.

FIGURE 1.

Recapitulating, Wrangham et al. [1] recently reported that chimpanzees' GHC-style preferences might be better explained by retention of matrilineal styles than group-level social learning mechanisms. Our results, however, suggest that at least in captive populations, chimpanzees may spontaneously extend their social learning efforts beyond family units, thus creating the within-group homogeneity and between-group heterogeneity in trait expression characteristic of cultural diversity [11]. Contemplating the discrepancy between Wrangham et al. [1]'s findings and ours, we suggest that potentially a higher frequency of group fusions in the Chimfunshi compared to the Kanyawara populations may account for the extended social learning tendencies in our study. The Chimfunshi chimpanzees are supplementary provisioned once a day, causing the entire group to retreat from the bush and congregate in a

relatively small space. In anticipation of the provisioning, the chimpanzees typically engage in GHC behavior relatively frequently (unpublished data). In conjunction, these aspects may create the conditions in which social learning may readily extend beyond family units. Alternatively, given the existing evidence for intraspecific variation in social tolerance across groups of chimpanzees [12], we hypothesize that differences in group cohesion between the Kanyawara and Chimfunshi communities may account for the respective discrepancy. This hypothesis is supported by the fact that group-level GHC-style convergence at Chimfunshi was highest in the most socially tolerant group (cf. [2, 12]). We extend Wrangham et al. [1]'s conclusion that it remains an exciting endeavor to investigate the underlying mechanism(s) guiding group-level convergence of socially-acquired behavior in chimpanzees. Notably, this mechanism does not need to be "conformity" but could be any (set of) mechanism(s) leading to within-group convergence (see group 2, also in [2]) and/or between-group divergence [13].

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150 **Figure legends**

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152 **Figure 1**. Proportion of individuals' engagement in palm-to-palm handclasping (*y*-axis) for
153 two isolated groups of chimpanzees (separated by vertical dotted line). Each box represents
154 one matriline and the size of the matrilineal units is indicated above the *x*-axis. Medians of
155 each matriline are represented by the solid, horizontal lines within the boxes, which represent
156 the range in PPC preference of each matriline. Circle area corresponds to the number of
157 observations contributing to one individual's PPC score.

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Author contributions

Conceptualization, E.J.C.v.L.; Methodology, E.J.C.v.L., and R. M.; Writing – Original Draft, E.J.C.v.L.; Writing – Review & Editing, E.J.C.v.L., K.A.C., R.M., M.B., and D.B.M.H.

In brief

The style of high-arm grooming, or "grooming handclasp", in the Kanyawara chimpanzees has recently been shown to be consistent within matrilineal family units, but not beyond. Van Leeuwen et al. show that in other populations, style homogeneity extends beyond families, thus revealing chimpanzee handclasping to be a group-level cultural phenomenon.